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Legume species differ in the responses of their functional traits to plant diversity

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Abstract

Plants can respond to environmental impacts by variation in functional traits, thereby increasing their performance relative to neighbors. We hypothesized that trait adjustment should also occur in response to influences of the biotic environment, in particular different plant diversity of the community. We used 12 legume species as a model and assessed their variation in morphological, physiological, life-history and performance traits in experimental grasslands of different plant species (1, 2, 4, 8, 16 and 60) and functional group (1 to 4) numbers. Mean trait values and their variation in response to plant diversity varied among legume species and from trait to trait. The tall-growing *Onobrychis viciifolia* showed little trait variation in response to increasing plant diversity, whereas the species with shorter statures responded in apparently adaptive ways. The formation of longer shoots with elongated internodes, increased biomass allocation to supporting tissue at the cost of leaf mass, reduced branching, higher specific leaf areas and lower foliar $\delta^{13}\text{C}$ values indicated increasing efforts for light acquisition in more diverse communities. Although leaf nitrogen concentrations and shoot biomass:nitrogen ratios were not affected by increasing plant diversity, foliar $\delta^{15}\text{N}$ values of most legumes decreased and the application of the ^{15}N natural abundance method suggested that they became more reliant on symbiotic N_2 fixation. Some species formed fewer inflorescences and delayed flowering with increasing community diversity. The observed variation in functional traits generally indicated strategies of legumes to optimize light and nutrient capturing, but they were largely species-dependent and only partly attributable to increasing canopy height and community biomass with increasing plant diversity. Thus, the analysis of individual plant species and their adjustment to growth conditions in communities of increasing plant diversity is essential to get a deeper insight into the mechanisms behind biodiversity–ecosystem functioning relationships.

51 **Key words:** biodiversity, functional traits, legumes, species identity, trait variation

Introduction

Growing awareness of widespread reductions in species diversity during the last decades has stimulated intensive research on the consequences of these changes on ecosystem functioning. A number of experimental studies in grassland ecosystems suggest strong and consistent positive effects of biodiversity on several ecosystem processes, e.g. primary productivity or nutrient cycling (see reviews in Hooper et al. 2005, Balvanera et al. 2006). In spite of evidence that complementarity among species contributes to positive biodiversity–ecosystem functioning relationships (Cardinale et al. 2007), the biological mechanisms subsumed under the term “complementarity” are not well understood. Diversity in functional characteristics is generally regarded to increase complementary use of essential resources such as light, water, carbon dioxide, minerals, and space among plant species in a community (Walker et al. 1999, Díaz and Cabido 2001). Resource-use efficiency measured at the community level on average increases with species richness and results in increased community biomass, canopy density and height (Spehn et al. 2000, Lorentzen et al. 2008) and soil nutrient exploitation (Palmberg et al. 2005, Oelmann et al. 2007). However, not all species contribute equally to the overall positive effects of biodiversity on primary productivity, rather some species may overyield whereas others may underyield in plant communities of increasing diversity (e.g. Hector et al. 2002, van Ruijven and Berendse 2003, Roscher et al. 2007).

Species performance is the net result of a number of morphological, physiological and phenological traits (= functional traits) operating from the cell to whole-plant level (Violle et al. 2007). Environment-induced trait variation (= phenotypic plasticity) is well known as the strategy by which plants maximize their performance under different abiotic and biotic conditions (e.g. Bradshaw 1965, Schlichting 1986, Schmid 1990). Nevertheless, adjustment of a trait is not necessarily adaptive, because it may be due to genetic correlation with other traits or may be a consequence of passive reductions in growth due to resource limitations (van

Kleunen and Fischer 2005). According to the “optimal allocation theory” (Bloom et al. 1985, McConnaughay and Coleman 1999), plants tend to adjust their allocation and invest a higher proportion to organs that optimize the acquisition of the most limiting resource. In addition, perennial species often reduce their allocation into reproductive structures in response to resource limitation (Chiariello and Gulmon 1991).

So far the relationship between plant community diversity and variation in plant functional traits has attracted little attention in the increasing effort to understand the positive effects of plant species diversity on ecosystem processes (Callaway 2007). In the present study carried out in a large biodiversity experiment located on a nutrient-rich floodplain site (Jena Experiment, Roscher et al. 2004) we focus on legumes, which are often considered as a relatively homogeneous plant functional group in grasslands. They are unique in their ability to fix symbiotically atmospheric nitrogen. Several biodiversity experiments have shown that legumes are keystone species in generating the observed biodiversity effects on ecosystem processes (Hooper et al. 2005). Nevertheless, effects associated with legume presence are highly variable, probably due to the identity of particular legume species and different environmental conditions (Spehn et al. 2002). In temperate grasslands, light and nutrients are among the most limiting factors that affect plant growth. Increasing canopy height and productivity at the community level with increasing species richness alter the amount and quality of available resources for individual species within these communities. Although legumes do not directly depend on the available soil nitrogen, the rates of energy-demanding N_2 fixation may be reduced under high soil nitrogen supply (Marschner 1995). Thus, we recorded data on shoot morphology, biomass allocation to different aboveground plant organs and measured leaf and shoot nitrogen concentrations as traits which were supposed to reflect strategies of light and nitrogen acquisition and retention by individual plants and may indicate changes in the growth environment. We used foliar C isotope ratios ($\delta^{13}C$) as integrated long-

term measure of photosynthetic activity and stomatal conductance, which depend on light availability, air humidity and plant nutritional status (Farquhar et al. 1989). We determined foliar N isotope ratios ($\delta^{15}\text{N}$) and applied the ^{15}N natural abundance method (Amarger et al. 1979) to assess plant diversity effects on N_2 fixation in legumes. In addition, we studied legume plant characteristics that may serve as indicators for plant individual performance such as shoot biomass or number of inflorescences. We related these plant characteristics to plant diversity — in terms of species and functional group richness — and community characteristics — in terms of canopy height and community biomass. We tested the following hypotheses: (1) Increasing plant diversity affects variation in trait values associated with strategies in light and nitrogen acquisition and retention. (2) Plant diversity effects are partly but not fully mediated by concomitant increases in community biomass and canopy height. (3) Plant diversity effects on trait variation vary among legume species, suggesting different strategies of species to respond to their biotic environment in ways which may increase complementary resource use.

Material and methods

Experimental set-up

The study was carried out as part of the Jena Experiment, a large integrated biodiversity experiment started in 2002 (Roscher et al. 2004). The experimental site lies in the floodplain of the river Saale near to the city of Jena (Thuringia, Germany, 50°55'N, 11°35'E, 130 m a.s.l.) and was used as an agricultural field for 40 years prior to the establishment of the biodiversity experiment. The area around Jena has a mean annual air temperature of 9.3 °C and a mean annual precipitation of 587 mm (Kluge and Müller-Westermeier 2000). The soil of the experimental site is a Eutric Fluvisol developed from up to 2 m thick loamy fluvial

sediments. Due to flooding dynamics, soil texture ranges from sandy loam near the river to silty clay with increasing distance from the river.

Sixty grassland species typically occurring in Central European semi-natural, species-rich grasslands (*Arrhenatherion* alliance according to the vegetation classification of Ellenberg, 1988) were selected as species pool for the experiment. Species were divided into four functional groups following the results of a cluster analysis with a literature-based trait matrix: grasses (16 species), legumes (12 species), small herbs (12 species) and tall herbs (20 species). The design of the Jena Experiment ensures that the presence/absence of each functional group (FG) is minimally confounded with species number (SR, see Roscher et al. 2004). In total, the main experiment comprises 82 plots of 20×20 m size: 16 monocultures (1 FG), 16 two-species mixtures (1 or 2 FG), 16 four-species mixtures (1 to 4 FG), 16 eight-species mixtures (1 to 4 FG), 14 sixteen-species mixtures (1 to 4 FG) and four replicates with a mixture of the complete species pool. The number of replicates with sixteen species was lower because pure legume or small herb mixtures were not possible at this species-richness level. Particular species compositions were compiled by independent random draws with replacement. In addition, all species were established in replicated monocultures of 3.5×3.5 m. Sown density aimed to establish 1000 seedlings per m^2 in a substitutive design, in which constant total density was achieved by reducing sowing densities of individual species according to the number of species in the mixture (Jolliffe 2000). Number of sown seeds was adjusted for germination rates from preliminary laboratory tests. Plots were grouped into four blocks parallel to the river, each of them containing the same number of experimental communities per species-richness level. All plots were mown twice a year in early June and September corresponding to the typical management regime for extensive meadows in the region and were not fertilized during the experimental period. Plots were weeded twice per growing season when the vegetation was low and the canopy not completely closed (early

April at the beginning of the growing season and early July after mowing). For further details see Roscher et al. (2004).

Data collection

In this study we analysed all legume species belonging to the experimental species pool (Table 1). Plant modules (individual shoots) served as basic unit for all measurements because the ability of some legume species to grow with above- or belowground runners hampers a distinction of plant genets in dense vegetation. Modules are defined as plant parts that would be able to grow independently if separated from the genet, the plant individual derived from a sexually produced seed (Harper 1977, Schmid 1990). The section of a creeping shoot between two nodes and the leaf formed at the distal node was considered as a module in the case of *T. repens*. All data are based on two 10-day harvest periods during early and late summer 2006 (June, August) at estimated peak biomass before mowing. Two legumes with an annual overwintering life cycle, *T. campestre* and *T. dubium*, were only investigated during the first harvest period because no adult plants were available in late summer.

In each plot where legumes were growing, five modules per species were randomly chosen along transects divided into regular sections (of 50 and 25 cm length in large and small plots, respectively). In the field, module height and canopy height of the immediately surrounding vegetation were determined. Module number per genet was counted for species where genets could be distinguished from each other. The selected modules were cut off near the ground, put in sealed plastic bags and transported in a cool box to the laboratory. The following standard protocol was used for further sample preparation. Stretched module length (= maximum shoot length) and internode length of 3 to 5 internodes in the central part of the main shoot axis were measured. Modules were separated into compartments (supporting parts: stems and secondary axes; leaves; reproductive parts: inflorescences and fruits).

Secondary axes, higher-order axes and inflorescences were counted. Phenology was assessed on a nine-part scale according to different stages of flower and fruit development. Three to ten (dependent on leaf size and number) fully expanded leaves from the upper module part were chosen, and leaf area was measured immediately as part of the biomass separation process (LI-3100 Area Meter, LI-COR, Lincoln, U.S.). Petioles and rachis of compound leaves were included in leaf area measurements.

All plant material was dried (70°C, 48 h) and weighed. Leaf samples as well as the remaining plant compartments (= bulk samples per species and plot) were ground with a ball mill. Approximately 20 mg of this material was analysed for carbon and nitrogen concentrations with an elemental analyzer (Vario EL Element Analyzer, Elementar, Hanau, Germany). Nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) isotope ratios were measured from leaf material (3 mg and 0.8 mg, respectively) with an isotope-ratio mass spectrometer (Delta C prototype IRMS, Finnigan MAT); sample ratios of $^{15}\text{N}/^{14}\text{N}$ are given relative to the international standard for atmospheric N_2 , and sample ratios of $^{13}\text{C}/^{12}\text{C}$ refer to the VPDB standard for C. Values are expressed in per-mil relative to the standards. To assess N_2 fixation of legumes with the ^{15}N natural abundance method (Amarger et al. 1979), *Lolium perenne* L. (sown as additional species into a small area of all large experimental plots; Roscher et al. 2008) and *Taraxacum officinale* Wiggers (included in the experimental species pool and occurring as a weed in near all plots where the species was not sown; Roscher et al. 2009) were used as non- N_2 -fixing reference species. Leaf material of these species collected during both harvest campaigns in all large plots, where these species were available, was analysed for $\delta^{15}\text{N}$. The ^{15}N abundances in legumes and reference species were used to calculate the proportion of legume N derived from the atmosphere (pNdfa) as

$$\text{pNdfa} = (\delta^{15}\text{N}_{\text{ref}} - \delta^{15}\text{N}_{\text{legume}}) / (\delta^{15}\text{N}_{\text{ref}} - \text{B}) \quad (\text{eq. 1}),$$

where $\delta^{15}\text{N}_{\text{ref}}$ and $\delta^{15}\text{N}_{\text{legume}}$ are the ^{15}N abundances in the reference species and the N_2 fixing

legume species (Amarger et al. 1979, Högberg 1997). B values describing the $\delta^{15}\text{N}$ of the N_2 -fixing species when grown with N_2 in air as the sole N source were set to the lowest detected $\delta^{15}\text{N}$ for each legume species (Hansen and Vinther 2001, Carlsson et al. 2009). Foliar $\delta^{15}\text{N}$ values of the reference species *L. perenne* and *T. officinale* varied depending on spatial location of the experimental plots at the field site (using block identity and geographic coordinates as explanatory terms) and decreased with sown species richness (Appendix Fig. S1 in Supplementary Material). The dependence on plot location may be due to spatial variation in soil $\delta^{15}\text{N}$ at the field site. Declining foliar $\delta^{15}\text{N}$ values with increasing species richness might indicate a shift in the uptake of different N forms, an increasing transfer of N from legumes to co-occurring plants or a larger amount of soil N deposited by legume plants via rhizodeposition or degradation of legume litter (Högberg 1997). Because the mechanisms causing a decrease in $\delta^{15}\text{N}$ values of reference species with increasing species richness or affecting their spatial variation across the field site equally apply to legumes themselves, pNdfa was only calculated if $\delta^{15}\text{N}$ values of reference species growing at the same plot were available. Therefore, small monoculture plots of legumes were excluded from these calculations. Differences in foliar $\delta^{15}\text{N}$ between the reference species were not statistically significant. Thus, pNdfa obtained with either *L. perenne* or *T. officinale* as reference species were used in cases where only one of these species was available and values were averaged in plots where both species could be sampled.

Community biomass was recorded in each plot in 20×50 cm rectangles shortly before mowing. Two randomly allocated samples were taken in small plots, and four samples were harvested in large plots. Plant material was cut 3 cm above ground, dried (70°C , 48 h) and weighed.

Data analyses

All trait values were averaged per species and plot for each harvest campaign. Derived variables for further analyses are summarized in Table 2. Measurements of *T. fragiferum* were excluded from all analyses because this species was extinct in a large number of plots (Table 1). Data were analysed with mixed-effects models using the *nlme* package of the statistical software R2.6.2 (R Development Core Team, <http://www.R-project.org>). Although the Jena Experiment has a factorial design based on gradients of species and plant functional group richness, the random species allocation to each mixture led to unbalanced occurrences of individual species in the experimental plots that violate the assumption of independence of errors. Mixed-effects models account for this non-independence of errors by modelling the covariance structure given by the random effects as grouping variable (Crawley 2002). Block and plot identity were entered as random effects in a nested sequence. Starting from a constant null model we added the fixed effects sequentially. Firstly, we fitted plant diversity as species richness separated into a monoculture vs. mixture contrast (Mo) and a log-linear term (SR), and functional group number (FG). Secondly, legume species identity (ID) was entered. In the following steps we fitted interaction terms between species identity and the experimental factors ($ID \times Mo$, $ID \times SR$, $ID \times FG$), season (June, August) and interaction terms between season and the previously mentioned terms. We applied the maximum likelihood method and used likelihood ratio (L) tests to assess the statistical significance of model improvement. In alternative models we changed the fitting order of the experimental factors SR and FG because of the slight non-orthogonality between them. However, both fitting sequences yielded very similar results. Furthermore, we tested whether plant functional group composition (presence and absence of grasses, small herbs and tall herbs) explained additional variation in trait values. Because we only rarely observed effects of these explanatory terms, we do not present the corresponding results. To test whether effects of species and functional group number on the values of legume traits operated in an indirect

way via increasing the canopy height or community biomass, we fitted these plant community characteristics as covariates before the experimental treatments in a further set of models. R^2 statistics for the mixed models were calculated based on likelihood-ratio test statistics comparing the log-likelihood of the model after fitting the explanatory terms with the log-likelihood of the model excluding these terms (Magee 1990).

Finally we explored functional traits (excluding performance indicators such as module biomass and traits characterising reproduction) with standardized principal components analysis (PCA). We used the respective constrained ordination technique, redundancy analysis (RDA), with different combinations of explanatory terms and covariates, i.e. (1) species identity, (2) community diversity (monoculture vs. mixture contrast, log-linear species richness, functional group number), (3) canopy height and community biomass, and (4) season in partial analyses to decompose the variation in functional traits explained by each set of explanatory variables following the procedure described in Borcard et al. (1992). In addition, we tested whether the differential responses of individual species explained a further proportion of variation and fitted interaction terms of species identity with community diversity and season. Block and plot identity were always entered as covariates and restricted Monte Carlo tests (999 permutations) were applied to assess the significance of explanatory terms. Ordination analyses were performed with CANOCO 4.5 (ter Braak and Šmilauer 2002).

Results

Aboveground plant traits of shoots and leaves and performance traits in terms of biomass and investment into reproduction differed significantly among the investigated legume species. In addition, the different legume species varied in their responses to increasing species and functional group number, i.e. plant diversity (Table 3, Appendix Table S1, S2). Community

biomass increased from monocultures to mixtures ($L = 17.47$, $P < 0.001$) and with increasing species richness of mixtures ($L = 4.69$, $P = 0.030$). Community biomass before the first mowing was significantly higher than before the second mowing ($L = 31.08$, $P < 0.001$). Community biomass correlated positively with canopy height (May: $r = 0.712$, $P < 0.001$, $n = 57$; August: $r = 0.751$, $P < 0.001$, $n = 50$), which also increased from monocultures to mixtures ($L = 27.05$, $P < 0.001$) and with increasing species richness of mixtures ($L = 6.86$, $P < 0.001$).

In the following we (1) highlight the most significant effects of plant diversity on trait values of legumes, (2) assess whether the mechanism by which plant diversity affects trait values is primarily due to a diversity-induced change in canopy height or community biomass, or (3) whether there are additional significant direct effects of plant diversity on species-specific differences among legumes which cannot be explained by (2). We were particularly interested in trait variation potentially reflecting different strategies of light and nitrogen acquisition and retention among species.

Legume positioning within the canopy (relative growth height)

On average, relative growth height of legumes, i.e. module height compared with the surrounding vegetation, was significantly less than 1 in early summer (one-sample t-tests, $P \leq 0.050$) except for *O. viciifolia* with a relative growth height not significantly different from 1 ($t_{14} = 0.547$, $P = 0.593$). In late summer relative growth height of *O. viciifolia* even exceeded canopy height (of all neighboring species) in mixtures ($t_{14} = 4.302$, $P = 0.001$), while relative growth height of the other legumes was mostly close to 1 ($P > 0.05$). Relative growth height generally decreased from monocultures to mixtures, which was primarily attributable to increasing canopy height and community biomass (Table 3; Fig. 1a, 2a, S2a). However, per-species analyses showed that plant diversity affected relative growth height of all species

except *O. viciifolia* not only via increased canopy height and community biomass (Table S2).

Legume performance in terms of biomass and investment into reproduction

On average, module mass of legumes did not change in response to plant diversity because some species had lower module mass in monocultures than in mixtures and increased module mass with increasing species richness of mixtures whereas other species showed the opposite or no relationships (see significant interactions “ID × Mo”, “ID × SR”; Table 3, S2; Fig. 1b, S2b). Canopy height and community biomass affected module mass of legumes independently of plant diversity, which had a significant direct effect even after fitting the covariables. Module numbers per genet, counted for species with clearly distinguishable plant genets only, were lower in mixtures than in monocultures, again irrespective of changes in community characteristics described by the covariables (Table S1), however, this effect was not significant in separate analyses for each individual species (Table S2).

Overall, the number of inflorescences per module decreased with increasing species richness, but the response of individual species varied greatly (Table S1, S2). Flower or fruit development was generally more advanced in monocultures than in mixtures of increasing species richness (Table S1). This negative effect of mixture environment on reproductive phenology was mainly due to increasing canopy height and community biomass.

Shoot and leaf morphology

Legumes growing in mixtures generally invested more biomass into supporting tissue (stems, secondary axes) at the cost of leaf mass, resulting in lower leaf:stem ratios in mixtures of increasing species richness (Table 3; Fig. 1c). Only two legume species, *M. lupulina* and *O. viciifolia*, did not change the investment into stems and leaves when growing in mixtures or in response to increasing species number in mixtures (Table S2). The number of secondary axes

generally did not vary in response to community diversity, but individual species differed in their response to some degree (significant interaction “ID \times Mo”; Table S1). Four species produced shoots with fewer secondary axes either in mixtures compared with monocultures or with increasing species number in mixtures (Table S2). Shoot length of all species except for *O. viciifolia* and *V. cracca* increased from monocultures to mixtures or with increasing species number in mixtures (Table 3, S2; Fig. 1d, S2d). The formation of longer shoots was mostly correlated with elongated internodes on the main axes (Table S1, S2). All species except *O. viciifolia* increased the SLA from monocultures to mixtures or with increasing species or functional group numbers in mixtures (Table 3, S2; Fig. 1e, S2e). Plant diversity effects on shoot and leaf morphology were due to increasing canopy height and community biomass, but significant interactions between species identity and plant diversity (“ID \times Mo”, “ID \times SR”, “ID \times FG”, Table 3, Fig. 2c-e) remained even after fitting these covariables. This suggested that variation of morphological traits in response to plant diversity differed among the studied legumes.

Leaf nitrogen and isotopic signatures

The relationship between mass-based leaf nitrogen and species richness largely depended on species identity (Table 3; Fig. 1f, S2f). Leaf nitrogen concentrations were either reduced (three legume species), increased (two legume species) or did not change in response to species or functional group richness (Table S2) and were not influenced by canopy height or community biomass.

Foliar $\delta^{15}\text{N}$ values of legumes declined from monocultures to mixtures, with increasing species numbers in mixtures and when mixtures were composed of species belonging to different functional groups (Table 3, Fig. 1g, S2g), but significant interaction terms with species identity indicated differential effects of plant diversity on foliar $\delta^{15}\text{N}$ values of the

various legume species (Table S2). Although canopy height and community biomass had significant effects on foliar $\delta^{15}\text{N}$ values (Fig. 2g, Table 3), these variables only partly explained plant diversity effects. On average, foliar $\delta^{15}\text{N}$ values of legumes were significantly lower in early summer than in late summer, but these seasonal differences varied among species (Table S2). In contrast, foliar $\delta^{15}\text{N}$ values of two non- N_2 -fixing reference species did not differ significantly between early and late summer (paired t-tests $p > 0.05$; *L. perenne* $\delta^{15}\text{N} = 1.91 \pm 0.84\text{‰}$ SD, *T. officinale* $\delta^{15}\text{N} = 1.90 \pm 1.09\text{‰}$). Proportions of N derived from N_2 fixation (pNdfa) calculated based on the ^{15}N natural abundance method with *T. officinale* and *L. perenne* as reference species, where these reference species were available, differed significantly among legume species ($L = 44.15$, $P < 0.001$). The proportion of N derived from N_2 fixation increased with increasing species numbers in mixtures ($L = 10.42$, $P = 0.012$, Fig. 3), and increasing functional group number ($L = 5.77$, $P = 0.016$); it was higher in early summer than in late summer ($L = 23.27$, $p < 0.001$; June 0.80 ± 0.16 , August 0.70 ± 0.22 averaged across species and plots).

Foliar $\delta^{13}\text{C}$ values decreased from monocultures to mixtures and species-specific values became lower in mixtures of increasing species or functional group number in most legume species (Table 3; Fig. 1h, S2h) except for the tallest species *M. × varia* and *O. viciifolia* (Table S2). Unexpectedly, averaged across all species, foliar $\delta^{13}\text{C}$ values decreased when foliar N concentrations increased (Pearson correlation coefficient for early summer: $r = -0.412$, $P < 0.001$, $n = 132$; for late summer: $r = -0.260$, $P = 0.004$, $n = 119$), while significant correlations for individual species were rare. Relative module height as surrogate for legume positioning within the canopy was positively related to foliar $\delta^{13}\text{C}$ values averaged across all species (Pearson correlation coefficient for early summer: $r = 0.540$, $P < 0.001$, $n = 132$; for late summer: $r = 0.527$, $P < 0.001$, $n = 119$) and was often correlated in analyses of individual species as well.

Nitrogen utilization (module biomass:N ratio)

Variation in biomass:N ratios at the whole-shoot level in response to plant diversity varied largely among legume species (Table 3, Fig. 1i, S2i) with significant effects in nine species (Table S2). Increasing canopy height and community biomass led to increased shoot biomass:N ratios independent of variation in plant diversity (Fig. 2i).

Patterns of seasonal variation

Values of all traits except for inflorescence number per module differed between measurement dates (early June vs. August; Table 3, S1; Fig. S3). Relative module height, leaf:stem ratio, mass-based leaf nitrogen, foliar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ achieved larger values later in the growing season. In contrast, module mass, shoot length, SLA and module biomass:N ratios had larger values before first mowing. Seasonal variations in SLA and foliar $\delta^{13}\text{C}$ were mediated by variation in community characteristics between early and late summer, while canopy height and community biomass only partly explained seasonal variation in other traits.

Multiple trait analysis

The three leading axes of the principal components analysis accounted for 67 % of total variation in legume functional traits (first axis 29 %, second axis 22 %, third axis 16 %). The first axis had high loadings for traits related to plant height, i.e. shoot length, internode length, and module biomass:N ratios. This axis separated *O. viciifolia* from the other legumes. The second axis was characterized by traits related to species positioning in the canopy, i.e. SLA, foliar $\delta^{13}\text{C}$ values, and relative module height, while the third axis accounted for variation in mass-based leaf nitrogen and number of secondary axes per shoot. Redundancy analysis (RDA) showed that functional traits were significantly related to the explanatory variables

which were included in a model that accounted for 44.9 % of the total variation. The partition into different sets of explanatory variables indicated a large effect of species identity (explaining 33.8 % of variation) and a small, but significant effect of season (Fig. 4). While plant diversity and community characteristics together explained a significant proportion in trait variation, the decomposition of these terms gave evidence that main effects of plant diversity on legume trait combinations were largely explained by canopy height and community biomass. That is, by increasing canopy height and community biomass, plant diversity affected these traits indirectly. Interactions of species identity with community diversity and season explained an additional proportion of variation (12.3 %) leaving in total 42.8 % of unexplained variation. These results underscore the differential responses of legume species to community diversity and across season.

Discussion

Variation in functional traits to optimize resource capture, to compete with neighbors and finally to produce seed or vegetative offspring are of major importance for the adjustment of plants to their abiotic and biotic environment (Schlichting 1986, Sultan 1995). It is known from many studies that plant species are plastic for numerous ecologically important traits including morphology, physiology, anatomy, development and reproduction (Bradshaw 1965, Sultan 2000, Valladares et al. 2007). These studies also reported large interspecific differences in trait variation, and correlations between traits may vary in different environments (Schlichting 1989). Therefore the study of a large set of traits is required to assess trait variation in relation to complex environmental changes, such as variation in plant diversity and species composition, which affects the availability of multiple resources at the same time.

In our study, we focused on traits measured on aboveground plant organs which are known as

indicators for strategies of light and nitrogen capturing, because these resources are among the most limiting factors for plant growth in temperate grassland. The complementarity hypothesis in biodiversity research suggests that positive diversity–productivity relationships are related to a more complete use of available resources due to diversity in plant functional characteristics and niche differentiation among species (Tilman et al. 1997). Competition for light and nutrients increases at higher productivity levels. To assess to which extent significant effects of plant diversity on trait variation of legumes were mechanistically explained by diversity-induced increases of canopy height and community biomass, i.e. generalised light competition, we compared the results of analyses unadjusted for these covariables with results of analyses adjusted for these covariables. When in addition to the indirect effect via the two covariables there was a “residual” direct effect of diversity, other covariables which were not measured and thus could not be included in the analysis must have been mechanistically involved in the effect. These residual direct effects were obviously not related to generalised light competition but mostly represented differential effects of plant diversity on the different legumes species and were probably related to increasing complementarity among legumes in resource acquisition and retention.

Nitrogen acquisition

Because of their ability to fix N_2 symbiotically, legume species are less reliant on growth-limiting soil nitrogen resources than other grassland species. However, the energy-consuming symbiotic N_2 fixation may be suppressed when alternative N sources decrease the need for symbiotically fixed N (Hartwig 1998, Carlsson and Huss-Danell 2003). Because the presence of non-fixing plants that deplete soil mineral nitrogen, or even directly receive nitrogen fixed by legumes by uptake of root exudates or from mycorrhizal links to legumes (Paynel et al. 2001, Govindarajulu et al. 2005), increases from legume monocultures to mixtures and in

mixtures with increasing species and functional group numbers, it is likely that legumes become more dependent on their symbiotic N source with increasing plant diversity. The application of the ^{15}N natural abundance method with non- N_2 -fixing reference species (*L. perenne*, *T. officinale*) to assess proportions of legume-N derived from N_2 fixation (pNd_{fa}) provided consistent evidence that legume dependence on symbiotic N source increased with increasing plant diversity. This variation was only partly driven by increasing community productivity and indicated that interactions between legumes and non-legumes were modulated through other plant-diversity related mechanisms (Fig. 3). In spite of this overall stimulating effect of plant diversity on N_2 fixation, pNd_{fa} values varied among legume species and were particularly high in the short-lived legumes *T. campestre* and *T. dubium* which probably have a lower ability to compete with established perennial species for soil nitrogen. The higher proportions of N derived from N_2 fixation in early summer — when experimental communities reached peak biomass — than in late summer before the second mowing — which correlated with higher leaf nitrogen concentrations and lower biomass:N ratios at the module level — gave further indication that legumes increased their reliance on N_2 fixation when competition for soil N was large.

Light acquisition

Our comparison of canopy height and plant height of individual legumes suggested that their access to direct insolation decreased with increasing plant community diversity, although we could not characterise the light climate experienced by the investigated plant individuals. All species except for the tallest, *O. viciifolia*, did not reach maximum canopy height in mixtures in early summer, whereas they did so in late summer (Fig. S2a, S3a). Canopy profiles are characterised by an exponential decrease of photosynthetic active radiation (Wacker et al. 2009) and changes in spectral light quality with a lower red to far red ratio deeper in the

canopy (Jones 1992). The disproportionate share of light obtained by larger plants increases the probability that smaller plants are outcompeted by shading (Weiner 1990). Our measurements at the whole-shoot and leaf level revealed that legume species in mixtures usually possessed typical strategies to tolerate or avoid lower light availability to a certain degree. They formed longer shoots with elongated internodes, reduced branching and invested more biomass into supporting tissue at the cost of leaf mass, all mechanisms known to enhance the chance to overtop neighbors in dense canopies (Smith 1982, Poorter and Nagel 2000). In addition, legumes generally increased their specific leaf area with increasing plant diversity, which is again a typical response of shaded plants (Corré 1983, Evans and Poorter 2001). Although variation in these traits differed among legume species, all of them except for the tall *O. viciifolia* increased shoot and internode length, had a lower leaf:stem ratio and increased SLA in relation to increasing species and functional group numbers (see Table 3).

A large amount of variation in these light acquisition traits probably represented generalized competition for light which was independent of the particular species contributing to it because it could be explained by the covariables canopy height and community biomass. Nevertheless, significant proportions of species-specific responses were attributable to residual direct effects of plant diversity not related to these covariables, suggesting that in addition to a generalized component of light competition there were also more specific components encapsulated in our plant diversity factors species richness and functional group number. Because these effects were different for the different legume species, they were probably related to complementary strategies of light acquisition. However, not all shade-avoidance reactions may reflect adaptive strategies, i.e. they may not always increase light acquisition and thus be mal-adaptive. A typical case occurs when the shade-avoidance reaction does not allow plant individuals to overtop their neighbors or reach canopy height (Weinig 2000). Although all legume species established successfully in all experimental plots

in the year of sowing in the Jena Experiment (unpubl. data), 4 years after sowing the smallest legume species with an annual overwintering or biannual life cycle, such as *M. lupulina*, *T. campestre* and *T. dubium* as well as the creeping *T. fragiferum*, went extinct in many experimental mixtures of higher species richness (see Table 1). This extinction is probably due to their non-sufficient genetic predisposition for adjustment or due to resource limitation of these species to adapt to canopy shade in multi-species mixtures. Even if smaller species may possess a larger trait variation, it might not be sufficient to increase competitiveness in plant communities of increasing diversity (Thein et al. 2008).

Foliar $\delta^{13}\text{C}$ values can give further information about plant positioning in the canopy. A wide range of physiological and biochemical processes affect isotopic composition of bulk samples: i) CO_2 source, ii) ratio of intercellular to ambient CO_2 concentrations (C_i/C_a) during assimilation, iii) metabolism and biosynthesis of carbon compounds, iv) cellular carbon budgets (Farquhar et al. 1989, Dawson et al. 2002). Thus, the carbon isotope composition of plants is jointly affected by the abiotic (e.g. irradiance, soil moisture, temperature, nitrogen nutrition) and biotic (e.g. leaf physiology, canopy height) environment of individual plants. In contrast to an expected positive correlation between $\delta^{13}\text{C}$ values and leaf nitrogen concentrations under a nitrogen limitation of C assimilation (Evans 1989), these variables varied largely independently at the species level in our study. Instead, plant canopy characteristics determined variation in foliar $\delta^{13}\text{C}$ values, although this relationship may have several causes. In contrast to studies of foliar $\delta^{13}\text{C}$ in previous biodiversity experiments (Caldeira et al. 2001, Jumpponen et al. 2005), canopy profiles measured in a 60-species plot in our experiment showed an increase in CO_2 concentrations with increasing canopy depth (unpubl. data). This CO_2 enrichment in lower canopies might be related to a decrease in $\delta^{13}\text{C}$ values of source CO_2 because soil respiration produces CO_2 with carbon isotope ratios similar to the substrate (Peterson and Fry 1987) and may affect foliar $\delta^{13}\text{C}$ of species growing in the

canopy (Farquhar et al. 1989, da Silveira et al. 1989). However, light availability and air humidity in lower canopy levels may also control C_i/C_a ratios *via* stomata aperture and hence affect $^{13}\text{C}/^{12}\text{C}$ ratios in leaf material. Foliar $\delta^{13}\text{C}$ values correlated with relative growth height of legume modules and were significantly higher in late summer when legumes reached a higher relative height than in early summer (Fig. S3h). In contrast, we found no diversity effects on foliar $\delta^{13}\text{C}$ values of the tallest legumes *M. × varia* and *O. viciifolia* indicating that light availability was a major control of carbon isotope discrimination, although we cannot exclude effects of source-air isotopic composition.

Fitness consequences

In our experiment, legumes mostly remained or even increased their performance at the module level assessed as module biomass in communities of increasing diversity. At the same time, plant genets often consisted of fewer modules in more diverse plant communities (except for *O. viciifolia*, *T. pratense*), indicating a decreasing performance at the genet level. Biomass allocation to reproductive compartments usually depends on plant size (Harper 1977). Reproductive structures have high resource costs and allocation into reproduction is generally greater under resource excess (Bloom et al. 1985). Therefore the observed reduction of inflorescence numbers in several legumes is not surprising, because it is likely that lower light availability — correlated with a decrease in legume module biomass (Table 3) — also affected the investment of legume species into reproduction.

Conclusions

So far, effects of community diversity on plant functional traits and their variation have received little attention although it is known that variation in physiological, morphological and life-history traits may alter direct and indirect interactions of organisms with their abiotic

and biotic environment (Callaway et al. 2003, Miner et al. 2005). Our study provided evidence for highly consistent effects of plant diversity on plant traits. Trait variation in particular of traits reflecting strategies for light acquisition were partly attributable to diversity-related changes in community characteristics in terms of canopy height and biomass production. However, plant diversity beyond these community characteristics was mainly responsible for species-specific trait variation of different legume species.

In our study we cannot differentiate whether variation of functional traits in legume species growing in plant communities of different diversity is exclusively due to phenotypic responses or whether different growing conditions led to local genetic differentiation at plot-scale, although each species was established with identical seed populations in all plots (Roscher et al. 2004). In addition, the potential plastic response of a species may be larger than what was observed, which might have been limited by resource availability (van Kleunen and Fischer 2005); and the number of replicates of particular legume species at each species-richness level was often small. Nevertheless, our study shows that the investigated legume species are neither redundant in their functional characteristics nor in the variation of these traits in relation to plant diversity. This is in line with previous studies at larger scales (Díaz et al. 2004). The uniqueness of species behavior shows that *a priori* classifications into functional groups are limited in their usefulness to elucidate biodiversity effects on ecosystem processes (Wright et al. 2005, McGill et al. 2006). Therefore, it is important to also consider potential particularities of individual species and interactions between individual species to better understand processes measured at the community level.

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Figure captions

Figure 1: Trait values plotted against sown species number. Trait values per species are averaged across different plots and season (June, August) for each species-richness level. Each regression line represents a legume species. For species symbols and line styles see Fig. 3.

Figure 2: Trait values plotted against canopy height including values measured in June (before first mowing) and August (before second mowing). Each regression line represents a legume species. For line styles see Fig. 3.

Figure 3: Proportion of N derived from N₂ fixation (pNdfa) based on the ¹⁵N natural abundance method plotted against sown species number. Values per species are averaged across different plots and season (June, August) for each species-richness level. Each regression line represents a legume species.

Figure 4: Summary of Redundancy Analysis (RDA) using different sets of explanatory variables in partial analyses to decompose their effects on legume trait variation. For each set of explanatory variables being species identity, season and plant community (separated into diversity and canopy height and community biomass, respectively) the proportion of explained trait variation, F ratio statistics and P values obtained by Monte Carlo tests (999 permutations) are shown. Shared variation indicates the proportion of explained variability that cannot be attributed uniquely to a certain set of predictor variables. An additional proportion of variation may be explained by differential responses of individual species (interactions of species identity with community diversity and season).

Figure 1

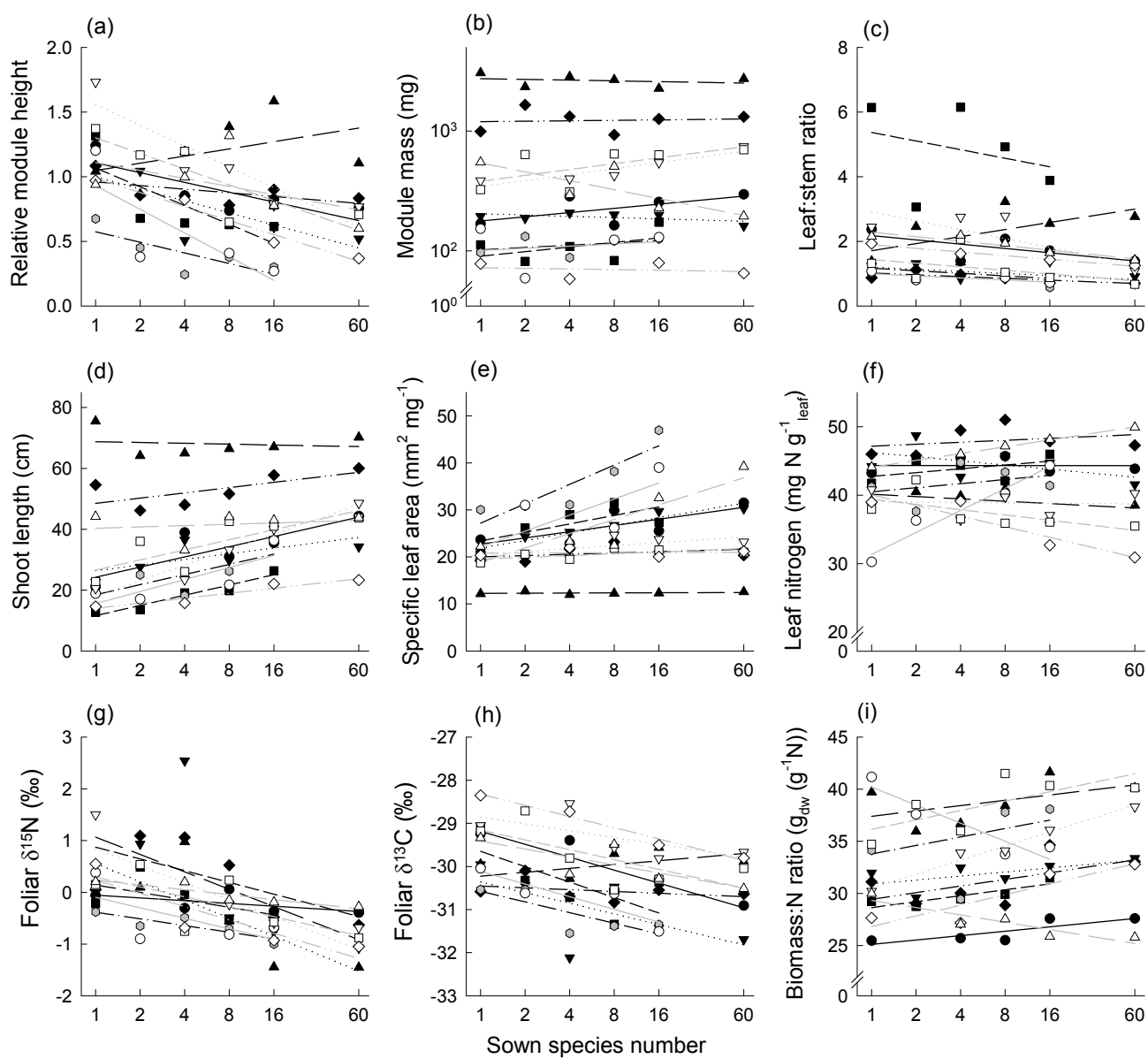


Figure 2

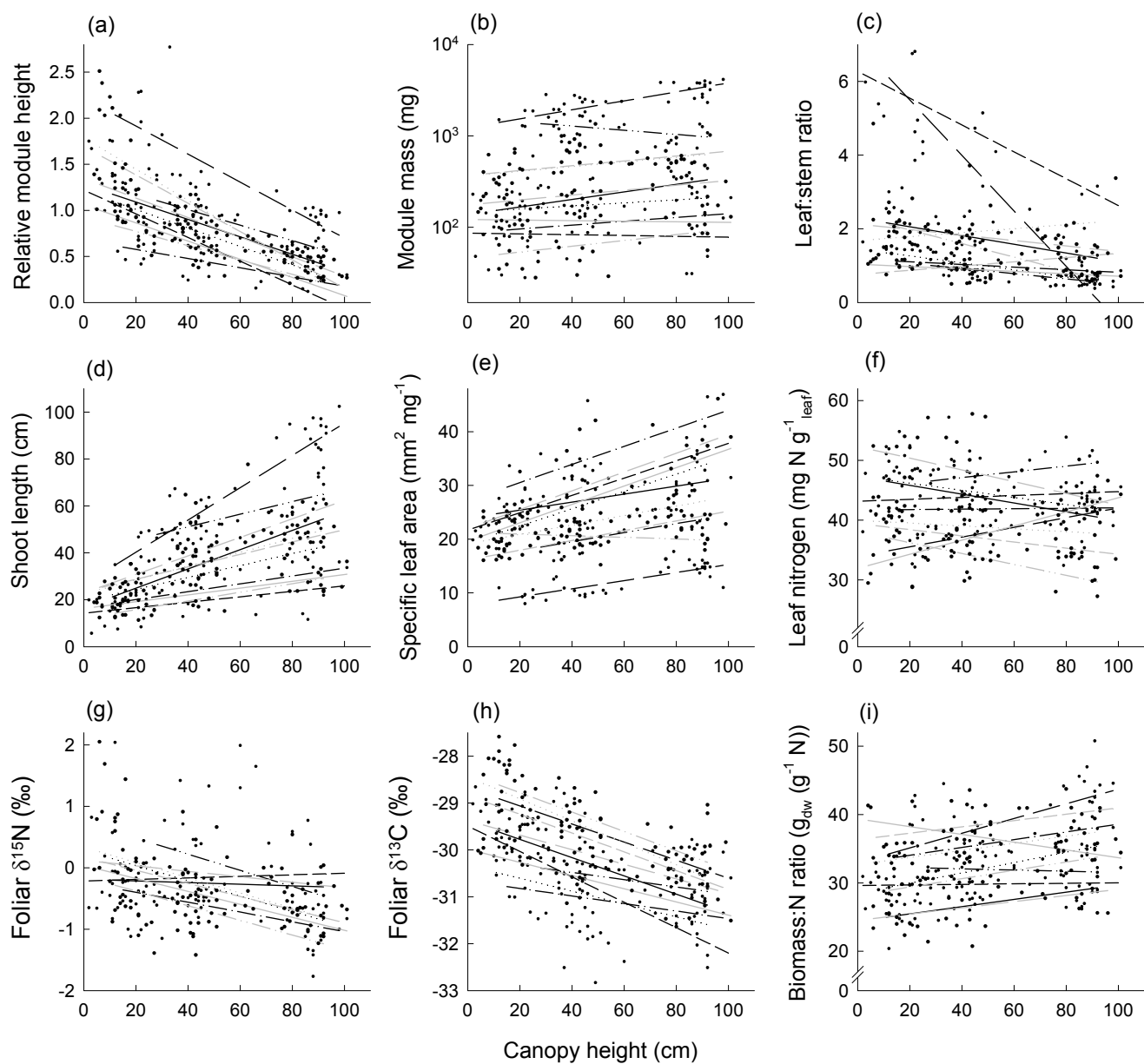


Figure 3

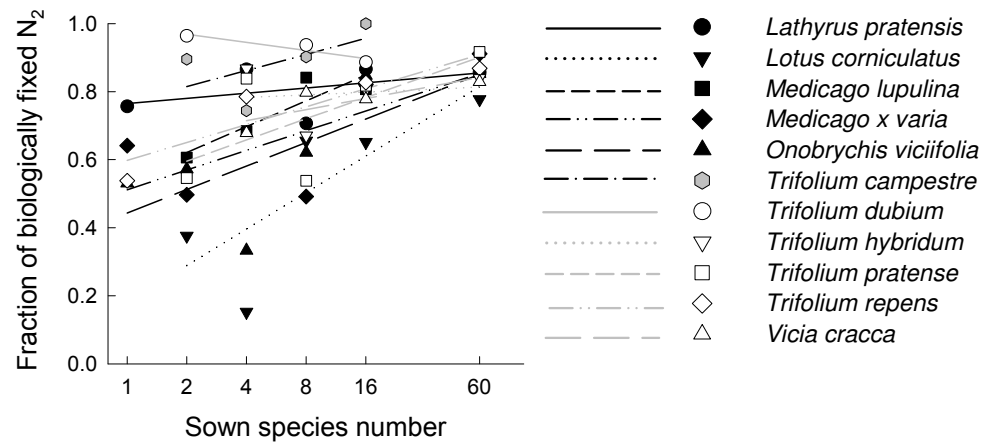


Figure 4

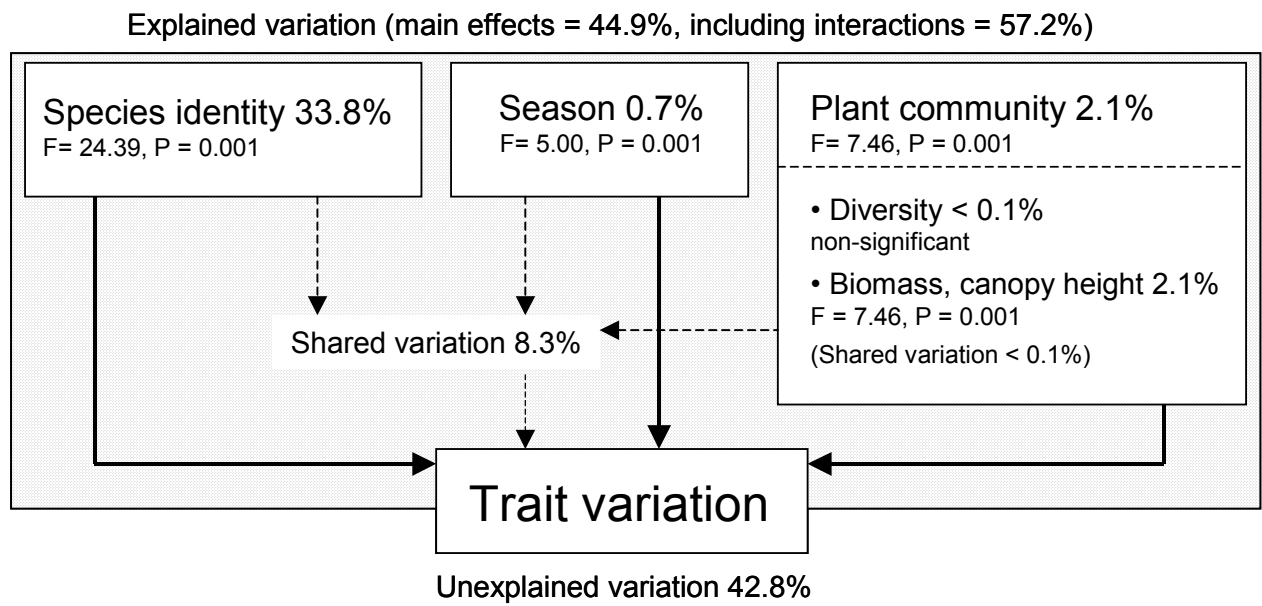


Table 1: Number of plots in which the investigated legumes occurred in the experiment. The number of plots in which the original seed mixtures contained the respective legume species is given in parentheses. Abbreviations for life cycle are: a = annual, ao = annual overwintering, p = perennial

Species	Life cycle	Species richness					
		1	2	4	8	16	60
<i>Lathyrus pratensis</i> L.	p	2 (2)	0 (0)	1 (1)	2 (2)	4 (4)	3 (3)
<i>Lotus corniculatus</i> L.	p	2 (2)	1 (1)	1 (1)	4 (4)	4 (4)	3 (3)
<i>Medicago lupulina</i> L.	ao, p	2 (2)	2 (2)	3 (3)	3 (4)	2 (2)	0 (3)
<i>Medicago x varia</i> Martyn	p	2 (2)	1 (1)	2 (2)	1 (1)	3 (3)	3 (3)
<i>Onobrychis viciifolia</i> Scop.	p	2 (2)	1 (1)	2 (2)	4 (4)	5 (5)	3 (3)
<i>Trifolium campestre</i> Schreb.	a, ao	2 (2)	1 (1)	1 (1)	2 (4)	1 (5)	0 (3)
<i>Trifolium dubium</i> Sibth.	a, ao	2 (2)	1 (1)	0 (0)	2 (3)	1 (3)	0 (3)
<i>Trifolium fragiferum</i> L.	p	1 (2)	0 (0)	1 (1)	1 (4)	0 (3)	0 (3)
<i>Trifolium hybridum</i> L.	p	2 (2)	0 (0)	1 (1)	4 (4)	5 (5)	3 (3)
<i>Trifolium pratense</i> L.	p	2 (2)	1 (1)	1 (1)	1 (1)	2 (2)	3 (3)
<i>Trifolium repens</i> L.	p	2 (2)	0 (0)	1 (1)	0 (0)	6 (6)	3 (3)
<i>Vicia cracca</i> L.	p	2 (2)	0 (0)	2 (2)	1 (1)	6 (6)	3 (3)

Table 2: Overview of traits investigated on aboveground plant organs in this study

Variable	Unit	Description
Relative module height	cm cm ⁻¹	Module height divided by canopy height of the surrounding vegetation
Module biomass	mg	Aboveground dry mass per module
Leaf : stem ratio	mg _{leaf} mg ⁻¹ _{stem}	Leaf dry mass per dry mass of supporting tissue
Shoot length	cm	Stretched module length
Specific leaf area (SLA)	mm ² _{leaf} mg ⁻¹ _{leaf}	Leaf area per leaf dry mass
Leaf nitrogen	mg N g ⁻¹ _{leaf}	Foliar nitrogen concentration (Nitrogen mass per leaf dry mass)
Biomass:N ratio	g _{dw} (g N) ⁻¹	Module biomass per unit nitrogen
Foliar δ ¹⁵ N	‰	¹⁵ N isotopic signature of leaves
Foliar δ ¹³ C	‰	¹³ C isotopic signature of leaves
Module number		Number of modules per plant individual
No. secondary axes		Number of secondary and higher order lateral axes per module
Internode length	cm	Length of the longest internode per module
No. inflorescences		Number of inflorescences per module
Phenology		Phenology of flower and fruit development (ordinal scale)

Table 3: Summary of mixed-effects model analyses of functional traits combining all legume species

Model	Relative height		Module mass		Leaf:stem ratio		Shoot length		Specific leaf area	
	A	B	A	B	A	B	A	B	A	B
	L ratio	p	L ratio	p	L ratio	p	L ratio	p	L ratio	p
R ² statistics	0.70	0.89	0.87	0.89	0.52	0.56	0.88	0.91	0.84	0.89
Canopy	--	141.62 ***↓	--	36.78 ***↑	--	16.61 ***↓	--	133.03 ***↑	--	53.04 ***↑
Biomass	--	5.52 *↓	--	4.63 *↑	--	1.68	--	16.85 ***↑	--	0.84
Mo	15.29 ***↓	0.26	0.60	0.08	0.34	1.53	10.21 ***↑	0.60	4.23 *↑	0.19
SR	2.25	1.01	1.07	0.27	5.13 **↓	1.66	11.10 ***↑	4.40 *↑	0.41	0.09
FG	0.24	0.82	0.85	0.76	1.11	0.84	1.76	1.81	<0.01	<0.01
ID	104.89 ***	156.21 ***	345.03 ***	325.99 ***	64.09 ***	65.78 ***	237.31 ***	234.52 ***	230.27 ***	266.33 ***
ID x Canopy	--	40.23 ***	--	16.04 .	--	23.92 **	--	15.43	--	42.36 ***
ID x Biomass	--	8.38	--	15.97	--	12.53	--	8.24	--	31.49 ***
ID x Mo	34.91 ***	17.11 .	33.01 ***	26.68 **	4.30	1.74	61.24 ***	27.45 **	29.22 **	5.87
ID x SR	5.00	11.44	26.00 **	34.90 ***	3.08	5.83	36.37 ***	45.36 ***	40.69 ***	41.39 ***
ID x FG	11.12	26.88 **	12.79	17.67 .	8.38	10.00	11.19	21.08 *	15.67	27.62 **
Season	64.54 ***A	2.93 .	43.74 ***M	34.00 ***M	17.42 ***A	11.01 ***A	116.15 ***M	26.96 ***M	43.09 ***M	0.02
Season x Canopy	--	65.36 ***	--	5.21 *	--	0.61	--	19.65 ***	--	2.00
Season x Biomass	--	0.12	--	0.40	--	1.31	--	0.34	--	0.62
Season x Mo	2.36	0.02	0.01	4.12 *	0.11	1.05	0.70	6.08 *	3.16 .	0.25
Season x SR	1.95	4.37 *	0.31	0.32	0.84	0.06	0.06	1.17	0.96	2.04
Season x FG	26.25 ***	0.76	3.30 .	3.68 .	0.04	0.03	3.02 .	1.53	1.36	0.43
Season x ID	36.91 ***	65.49 ***	43.28 ***	34.38 ***	81.73 ***	52.95 ***	51.23 ***	58.74 ***	91.24 ***	82.37 ***

Model	Mass-based leaf N		Foliar δ ¹⁵ N		Foliar δ ¹³ C		Biomass:N ratio	
	A	B	A	B	A	B	A	B
	L ratio	p	L ratio	p	L ratio	p	L ratio	p
Canopy	--	4.61	--	19.00 ***↓	--	83.70 ***↓	--	45.51 ***↑
Biomass	--	0.05	--	5.76 *↓	--	0.07	--	5.01 *↑
Mo	0.66	2.51	10.88 **↓	6.22 *↓	14.60 ***↓	3.17 .↓	0.69	1.12
SR	2.87 .↓	1.52	14.44 ***↓	11.04 ***↓	0.20	0.90	2.26	0.32

FG	0.11	0.10	9.23 **↓	10.13 **↓	0.04	0.20	0.01	0.08
ID	171.11 ***	168.60 ***	71.13 ***	67.94 ***	103.89 ***	117.73 **	231.14 ***	214.81 ***
ID x Canopy	--	46.06 ***	--	9.53	--	14.05	--	26.95 **
ID x Biomass	--	12.53	--	5.61	--	12.32	--	10.52
ID x Mo	25.90 **	14.71	22.91 *	27.14 **	24.79 **	19.57 *	35.19 ***	24.66 **
ID x SR	22.96 *	26.77 **	19.31 *	23.29 **	7.95	11.78	17.24	26.02 **
ID x FG	18.03	24.78 **	17.04	19.30 *	28.31 **	37.09 ***	19.43 *	26.01 **
Season	16.51 ***A	12.82 ***A	26.45 ***A	20.64 ***A	43.27 ***A	1.90	41.32 ***M	14.52 ***M
Season x Canopy	--	4.23 *	--	2.10	--	17.76 ***	--	1.24
Season x Biomass	--	0.12	--	1.55	--	3.40 .	--	0.47
Season x Mo	0.07	0.58	4.69 *	0.89	0.66	0.05	<0.01	0.07
Season x SR	0.13	0.11	7.68 **	12.03 ***	0.82	0.02	0.49	0.04
Season x FG	0.10	1.17	1.95	0.09	4.07 *	0.35	1.32	0.44
Season x ID	72.25 ***	40.50 ***	34.44 ***	31.95 ***	33.78 ***	28.86 **	56.19 ***	30.24 ***

Models were fitted by stepwise inclusion of variables. Listed are the results of likelihood ratio tests that were applied to assess model improvement (= L ratio), the statistical significance of the explanatory terms, where . $P \leq 0.10$, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$. R^2 statistics is based on likelihood ratio test statistics in comparison to the intercept-only model. The first columns for each trait show models (= model A) where only the experimental factors were fitted. They are followed by columns with models (= model B) where canopy height and community biomass were fitted before the experimental factors. Arrows indicate a significant increase (↑) or decrease (↓) of trait values with increasing community diversity, biomass or canopy height. J (= June) or A (= August) indicate a significant increase or decrease of trait values from the first to the second sampling period, respectively. Abbreviations: ID = species identity, Canopy = canopy height, Biomass = community biomass, Mo = monoculture vs. mixture contrast, SR = species number (log-scale), FG = functional group number, Season = time of sampling (early summer = June, late summer = August).

Supplementary online materialRoscher C, Schmid B, Buchmann N, Weigelt A, Schulze E-D. **Legume species differ in the responses of their functional traits to plant diversity**

Table S1: Summary of mixed-effects model analyses of functional traits combining all legume species

Model	Module number		No. inflorescences				Phenology				No. secondary axes				Internode length			
	A		B		A		B		A		B		A		B		A	
	R ²	L ratio	P	R ²	L ratio	P	R ²	L ratio	P	R ²	L ratio	P	R ²	L ratio	P	R ²	L ratio	P
Canopy	--	--		1.72	--		2.04	--		27.14 ***↓	--		51.25 ***↓	--		117.65 ***↑	--	
Biomass	--	--		4.33 *	--		2.61	--		10.34 **↓	--		9.16 **↓	--		29.29 ***↑	--	
Mo	3.90 *↓			6.28 *↓	2.24		0.92	3.06 ↓		0.66	0.37		2.20	6.11 *↑		1.94		
SR	0.53			1.05	5.51 *↓		5.04 *↓	3.50 ↓		0.44	<0.01		1.39	6.44 *↑		0.68		
FG	0.06			<0.01	0.08		<0.01	0.02		0.01	0.99		1.54	0.42		0.09		
ID	79.46 ***			72.50 ***	184.85 ***		190.03 ***	180.68 ***		177.89 ***	185.36 ***		186.34 ***	240.35 ***		215.43 ***		
ID x Canopy	--			7.11	--		68.29 ***	--		15.39 .	--		16.28 .	--		105.36 ***		
ID x Biomass	--			1.70	--		19.99 *	--		11.04	--		10.14	--		12.42		
ID x Mo	10.69			12.05 .	28.18 ***		40.34 ***	16.69		37.67 ***	13.09		24.27 **	40.92 ***		17.80 *		
ID x SR	5.72			7.75	8.76		21.39 *	12.47		29.48 ***	17.44 *		15.99 .	19.85 *		17.37 *		
ID x FG	11.54			19.74 **	8.51		22.80 **	10.09		15.59 .	9.49		14.98 .	11.01		10.65		
Season	16.90 ***M			23.74 ***M	3.51 .		0.01	63.89 ***A		50.67 ***A	63.05 ***A		4.43 *A	85.74 ***M		36.42 ***M		
Season x Canopy	--			6.35 *	--		5.00 *	--		4.88 *	--		14.56 ***	--		0.59		
Season x Biomass	--			0.46	--		0.11	--		0.50	--		0.11	--		6.01 *		
Season x Mo	0.04			2.59	3.23 .		<0.01	1.93		0.18	2.08		7.15 **	6.03 *		4.53 *		
Season x SR	<0.01			1.29	0.38		<0.01	0.20		0.49	5.95 *		0.28	0.07		0.18		
Season x FG	2.57			0.12	2.21		0.18	1.22		1.61	2.27		1.10	0.36		0.67		
Season x ID	27.71 ***			21.05 **	150.21 ***		82.73 ***	126.32 ***		82.05 ***	49.97 ***		53.91 ***	140.91 ***		55.33 ***		

Models were fitted by stepwise inclusion of variables. Listed are the results of likelihood ratio tests that were applied to assess model improvement (= L ratio) and the statistical significance of the explanatory terms, where . $P \leq 0.10$, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$. R² statistics is based on likelihood ratio test statistics in comparison to the intercept-only model. The first columns for each trait shows models (= model A) where only the experimental factors were fitted. They are followed by columns with models (= model B) where canopy height and community biomass were fitted before the experimental factors. Arrows indicate a significant increase (↑) or decrease (↓) of trait values with increasing community

diversity, biomass or canopy height. J (= June) or A (= August) indicate a significant increase or decrease of trait values from the first to the second sampling period, respectively. For abbreviations see Table 3.

Table S2: Summary of mixed-effects model analyses of functional traits per legume species

	Relative module height		Module mass		Module number		No. inflorescences		Phenology		Leaf:stem ratio		No. secondary axes		Shoot length		Internode length		Specific leaf area		Mass-based leaf N		Foliar $\delta^{15}\text{N}$		Foliar $\delta^{13}\text{C}$		Biomass:N ratio	
<i>Lathyrus pratensis</i>																												
Model	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
R ² statistics	0.44	0.84	0.75	0.78	NA	NA	0.59	0.70	0.55	0.57	0.60	0.87	0.51	0.67	0.80	0.86	0.81	0.86	0.45	0.73	0.53	0.62	0.56	0.82	0.56	0.74	0.54	0.80
Canopy	--	↓***	--	↑**	--	--	--	↓*	--	ns	--	↓***	--	ns	--	↑***	--	↑***	--	ns	--	ns	--	ns	--	↓**	--	↑**
Biomass	--	ns	--	ns	--	--	--	ns	--	ns	--	ns	--	↓*	--	ns	--	↑.	--	↑.	--	ns	--	ns	--	ns	--	↑*
Mo	↓*	ns	↑.	ns	--	--	↑*	ns	ns	ns	↓**	ns	ns	↓.	↑**	ns	↑**	ns	ns	ns	ns	↓*	ns	ns	↓*	↓*	ns	ns
SR	ns	.	↑.	ns	--	--	ns	ns	↓.	↓.	↓.	ns	ns	↓.	↑*	ns	↑.	ns	↑*	ns	ns	ns	ns	ns	↓*	↓.	ns	ns
FG	ns	ns	↑**	↑**	--	--	ns	ns	↓*	↓*	ns	ns	↓.	ns	ns	.	ns	ns	ns	↑.	ns	ns	↓**	↓**	↓*	↓*	ns	ns
Season	ns	*	**	*	--	--	***	**	ns	ns	ns	ns	*	ns	**	ns	***	*	ns	***	***	***	.	***	ns	ns	**	ns
Season x Canopy	--	*	--	ns	--	--	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	.	--	ns	--	*	--	*
Season x Biomass	--	ns	--	ns	--	--	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	*	--	ns	--	ns	--	.	--	**
Season x Mo	.	ns	.	*	--	--	*	***	ns	.	**	**	ns	ns	**	**	***	***	.	ns	ns	ns	ns	**	ns	ns	ns	.
Season x SR	ns	ns	ns	ns	--	--	ns	ns	.	ns	ns	***	ns	**	ns	.	ns	*	ns	ns	ns	ns	ns	*	ns	ns	ns	ns
Season x FG	ns	ns	*	*	--	--	ns	ns	*	.	ns	ns	.	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
<i>Lotus corniculatus</i>																												
Model	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
R ² statistics	0.77	0.94	0.46	0.54	0.53	0.68	0.30	0.34	0.38	0.39	0.63	0.77	0.58	0.69	0.68	0.79	0.82	0.88	0.62	0.71	0.65	0.73	0.66	0.72	0.47	0.72	0.72	0.87
Canopy	--	↓***	--	ns	--	ns	--	ns	--	ns	--	↓***	--	↓***	--	↑***	--	↑***	--	↑***	--	↓.	--	↓*	--	ns	--	↑**
Biomass	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	↓*	--	ns	--	↑*	--	ns	--	ns	--	↓.	--	ns	--	ns
Mo	↓**	ns	ns	ns	↓*	↓*	ns	ns	↓*	ns	↓*	ns	ns	↓**	↑**	ns	↑**	↑.	↑*	ns	ns	↓.	ns	ns	↓.	ns	ns	↑**
SR	↓*	ns	ns	↓.	ns	ns	ns	ns	↓*	↓*	ns	ns	ns	ns	ns	ns	↑.	ns	↑*	ns	↓**	↓.	↓**	↓**	ns	ns	↑*	ns
FG	ns	ns	ns	ns	↓.	↓*	ns	ns	ns	ns	ns	ns	ns	ns	↑.	.	ns	ns	ns	ns	ns	ns	↓**	↓*	↓*	↓*	↑*	ns
Season	***	ns	*	.	ns	ns	ns	ns	ns	ns	***	ns	***	ns	***	ns	***	***	***	ns	*	*	*	.	ns	.	***	*
Season x Canopy	--	***	--	ns	--	***	--	ns	--	ns	--	**	--	ns	--	*	--	ns	--	ns	--	**	--	*	--	ns	--	***

Season x Biomass	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	**
Season x Mo	ns	ns	*	*	**	ns	ns	ns	ns	ns	ns	ns	**	ns	ns	ns	**	*	ns	ns	**	ns	ns	ns	.	*	*	*
Season x SR	.	.	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	.	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns
Season x FG	*	ns	*	**	.	ns	ns	ns	ns	ns	ns	ns	ns	.	.	ns	ns	ns	ns	*	**	***	*	ns	ns	***	*	ns

Medicago lupulina

Model	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
R ² statistics	0.45	0.89	0.52	0.79	0.66	0.82	0.34	0.63	0.65	0.73	0.37	0.67	0.51	0.74	0.69	0.79	0.82	0.87	0.59	0.89	0.19	0.28	0.42	0.57	0.45	0.82	0.43	0.61
Canopy	--	↓***	--	ns	--	↓.	--	↓*	--	↓**	--	ns	--	↓.	--	↑.	--	↑*	--	↑***	--	ns	--	ns	--	↓***	--	ns
Biomass	--	ns	--	ns	--	ns	--	↓*	--	↓*	--	ns	--	ns	--	ns	--	ns	--	↑***	--	ns	--	ns	--	ns	--	ns
Mo	↓*	ns	ns	ns	↓*	↓*	ns	ns	ns	↓**	ns	ns	ns	ns	↑.	ns	↑**	ns	↑*	ns	ns	ns	ns	ns	↓*	↓.	ns	ns
SR	ns	ns	↑.	↑*	ns	ns	ns	ns	ns	ns	ns	ns	ns	↓.	↑**	↑**	↑***	↑**	ns	ns	ns	ns	↓.	↓.	ns	ns	*↑	↑*
FG	ns	↓*	ns	ns	ns	ns	ns	↓.	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	↓*	↓*	ns	ns	ns	ns
Season	ns	*	**	***	***	***	ns	ns	***	*	***	***	***	***	***	***	***	***	**	ns	ns	ns	.	*	ns	**	ns	*
Season x Canopy	--	ns	--	ns	--	*	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns
Season x Biomass	--	**	--	ns	--	ns	--	*	--	.	--	*	--	*	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns
Season x Mo	.	ns	ns	ns	ns	ns	*	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	.	ns
Season x SR	ns	*	ns	**	ns	**	ns	ns	ns	ns	ns	*	ns	.	.	**	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	*
Season x FG	.	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	**	ns	ns	ns	.	*	ns	ns	ns

Medicago x varia

Model	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
R ² statistics	0.80	0.90	0.34	0.45	0.60	0.67	0.80	0.85	0.78	0.91	0.67	0.82	0.83	0.86	0.59	0.80	0.71	0.83	0.65	0.88	0.25	0.66	0.52	0.58	0.19	0.84	0.31	0.49
Canopy	--	↓***	--	↓*	--	ns	--	ns	--	ns	--	↓***	--	↓.	--	↑***	--	↑***	--	↑**	--	ns	--	ns	--	↓*	--	ns
Biomass	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns
Mo	↓**	ns	ns	↓*	ns	ns	ns	↓*	ns	ns	ns	ns	ns	↓**	↑**	ns	ns	↑***	↑.	ns	ns	ns	ns	ns	ns	ns	ns	ns
SR	ns	↓**	ns	ns	↓**	↓***	ns	↓.	ns	↓.	↓**	*	ns	ns	ns	ns	↑*	ns	ns	↑***	ns	ns	↓***	↓***	ns	ns	↑*	↑*
FG	ns	ns	ns	ns	↓.	ns	↓*	↓***	↓.	↓*	ns	ns	ns	↓**	ns	ns	ns	**	↑**	↑*	ns	ns	ns	ns	ns	ns	ns	ns
Season	***	**	**	.	*	.	***	***	***	***	**	ns	***	***	*	ns	***	ns	***	ns	ns	ns	.	.	ns	ns	ns	ns
Season x Canopy	--	ns	--	ns	--	ns	--	.	--	***	--	**	--	ns	--	*	--	.	--	ns	--	ns	--	ns	--	ns	--	ns
Season x Biomass	--	ns	--	ns	--	ns	--	.	--	ns	--	ns	--	ns	--	ns	--	ns	--	***	--	*	--	ns	--	ns	--	ns
Season x Mo	ns	ns	ns	ns	ns	ns	ns	ns	ns	.	ns	**	ns	ns	.	**	*	ns	ns	ns	ns	**	ns	ns	ns	***	ns	.
Season x SR	*	ns	ns	ns	.	ns	ns	*	ns	ns	ns	ns	ns	*	ns	.	ns	ns	ns	ns	ns	.	ns	ns	ns	***	ns	ns
Season x FG	ns	ns	ns	ns	ns	.	**	ns	.	ns	.	ns	*	.	ns	ns	ns	*	ns	ns	ns	.	ns	ns	ns	ns	ns	ns

Onobrychis viciifolia

Model	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	
R ² statistics	0.52	0.92	0.51	0.62	0.29	0.42	0.72	0.79	0.37	0.46	0.46	0.77	0.49	0.60	0.74	0.84	0.77	0.88	0.66	0.66	0.44	0.52	0.66	0.76	0.62	0.80	0.61	0.62	
Canopy	--	↓***	--	↑***	--	ns	--	↑***	--	↓*	--	↓***	--	↓*	--	↑***	--	↑***	--	↑***	--	↓***	--	ns	--	↓***	--	↑***	
Biomass	--	**	--	ns	--	ns	--	ns	--	↓.	--	ns	--	↓*	--	↑*	--	ns	--	ns	--	ns	--	↓*	--	↓.	--	ns	
Mo	ns	ns	↑.	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	↓.	ns	ns	ns	ns	ns	ns	ns	↓.	↓.	ns	ns	ns	ns	
SR	ns	ns	ns	ns	ns	ns	ns	↓.	ns	ns	ns	ns	ns	↓.	ns	ns	ns	↓.	ns	ns	ns	↓.	↓***	↓***	ns	↓**	ns	↓.	
FG	ns	ns	ns	ns	ns	ns	↓*	↓.	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	↓.	ns	ns	ns	ns	ns	
Season	***	***	***	ns	ns	.	***	.	***	***	***	ns	***	***	***	**	***	***	***	***	***	***	ns	*	*	***	ns	***	*
Season x Canopy	--	*	--	ns	--	.	--	.	--	.	--	**	--	*	--	ns	--	ns	--	ns	--	ns	--	*	--	ns	--	ns	
Season x Biomass	--	ns	--	ns	--	ns	--	*	--	ns	--	***	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	
Season x Mo	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	*	ns	ns	ns	
Season x SR	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	**	**	ns	ns	ns	ns	
Season x FG	***	ns	.	ns	.	ns	**	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	.	ns	ns	
Trifolium campestre																													
Model	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	
R ² statistics	0.65	0.98	0.42	0.98	0.69	0.95	0.40	0.96	0.45	0.87	0.78	0.85	0.94	0.96	0.94	0.98	0.93	0.99	0.88	0.99	0.62	0.86	0.67	0.99	0.39	0.91	0.33	0.81	
Canopy	--	↓**	--	ns	--	↓**	--	ns	--	↓*	--	ns	--	ns	--	↑*	--	↑*	--	ns	--	ns	--	↓***	--	ns	--	ns	
Biomass	--	ns	--	↓.	--	↓.	--	↓*	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	↓.	--	ns	--	↓*	--	ns	
Mo	ns	↓**	ns	↓*	ns	ns	ns	↓*	ns	ns	ns	↓**	ns	↓**	ns	↑**	ns	↑**	ns	↑**	ns	ns	ns	↓**	ns	ns	↑.	↓*	
SR	ns	↓**	ns	ns	↓*	ns	ns	ns	ns	ns	↓*	↓*	↓***	↓**	↑***	↑**	↑***	↑*	↑***	↑*	ns	ns	ns	↓***	↓.	ns	ns	↓.	
FG	↓*	ns	↓.	↓***	ns	↓***	ns	↓***	ns	↓*	↓.	ns	ns	ns	ns	ns	ns	↑***	ns	↑***	ns	↓**	↓*	↓*	ns	↓**	↑.	↓.	
Trifolium dubium																													
Model	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	
R ² statistics	0.56	1.00	0.88	0.99	0.66	0.98	0.81	0.85	0.58	0.99	0.69	0.99	0.68	0.99	0.94	1.00	0.85	1.00	0.73	0.99	0.71	0.91	0.58	0.99	0.64	1.00	0.61	0.99	
Canopy	--	↓***	--	--	--	--	--	--	--	--	--	↓***	--	--	--	↑***	--	--	--	↑***	--	ns	--	--	--	↓***	--	↑***	
Biomass	--	--	--	↓***	--	↓.	--	↓*	--	↑***	--	--	--	↓**	--	--	--	↑***	--	--	--	--	--	↓***	--	--	--	--	
Mo	↓*	ns	ns	ns	↓*	↓**	ns	ns	↑*	ns	↓*	ns	↓*	ns	ns	ns	ns	ns	↑.	ns	↑.	ns	↓*	↓*	↓.	↓.	↑.	ns	
SR	ns	ns	↑**	ns	ns	ns	↓.	ns	ns	ns	ns	ns	ns	ns	↑**	ns	↑*	ns	ns	ns	↑.	ns	ns	↓**	ns	ns	ns	ns	
FG	ns	ns	↑*	ns	ns	ns	↓*	ns	ns	ns	↓.	ns	ns	↓*	↑**	ns	↑*	ns	↑*	ns	ns	ns	ns	↓**	ns	ns	ns	ns	
Trifolium hybridum																													
Model	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	
R ² statistics	0.84	0.94	0.51	0.56	0.55	0.78	0.69	0.72	0.86	0.89	0.54	0.64	0.52	0.59	0.79	0.87	0.78	0.81	0.66	0.75	0.19	0.26	0.64	0.66	0.73	0.88	0.64	0.68	
Canopy	--	↓***	--	↑**	--	↓*	--	↓***	--	ns	--	ns	--	↓***	--	↑***	--	↑***	--	↑***	--	ns	--	ns	--	↓***	--	↑*	

Biomass	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	↑*	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns
Mo	↓***	ns	ns	ns	↓.	ns	ns	ns	ns	ns	ns	ns	ns	ns	↑***	↑.	↑***	↑.	↑.	ns	ns	ns	↓***	↓***	↓.	ns	↑***	↑*
SR	↓.	ns	↑**	↑**	↓*	↓*	ns	ns	ns	ns	↓*	↓**	↓.	↓**	↑***	↑***	↑**	↑**	ns	ns	ns	ns	ns	ns	ns	ns	↑***	↑**
FG	ns	ns	ns	ns	ns	↓*	ns	ns	↓**	↓**	↓**	↓*	ns	ns	↑.	↑.	↑.	↑.	↑**	↑***	ns	ns	↓.	↓.	↓*	↓*	ns	↑.
Season	***	**	ns	ns	ns	***	***	***	***	***	.	*	***	ns	**	.	**	ns	***	ns	ns	ns	ns	*	***	ns	ns	ns
Season x Canopy	--	***	--	.	--	**	--	ns	--	ns	--	ns	--	ns	*	*	--	**	--	.	--	ns	--	ns	--	***	--	ns
Season x Biomass	--	ns	--	ns	--	ns	--	ns	--	ns	--	.	--	ns	--	.	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns
Season x Mo	ns	ns	**	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	***	ns	**	ns	ns	ns	ns	ns	*	ns	ns	**	ns	ns
Season x SR	*	ns	ns	ns	**	.	ns	ns	ns	**	*	.	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	.	ns	ns	ns
Season x FG	**	*	ns	ns	ns	ns	ns	ns	*	.	.	.	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	.	ns	ns	ns

Trifolium pratense

Model	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
R ² statistics	0.85	0.97	0.52	0.72	0.38	0.46	0.59	0.70	0.88	0.89	0.61	0.83	0.68	0.76	0.79	0.92	0.79	0.84	0.87	0.99	0.49	0.80	0.84	0.97	0.69	0.74	0.62	0.87
Canopy	--	↓***	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	↑***	--	↑**	--	↑***	--	↓*	--	↓.	--	↓***	--	ns
Biomass	--	ns	--	↓.	--	ns	--	↓.	--	↓*	--	↓*	--	ns	--	↑**	--	↑**	--	ns	--	ns	--	ns	--	↓*	--	ns
Mo	↓**	ns	↑*	↑*	ns	↓*	↑.	↑*	ns	↓*	ns	↓*	ns	↑**	↑**	↑**	↑**	↑*	↑*	ns	ns	ns	ns	ns	↓*	ns	↑**	↑**
SR	↓**	ns	ns	ns	ns	ns	ns	ns	ns	↓.	↓*	↓***	ns	ns	↑*	↑*	↑*	↑.	ns	ns	↓*	↓*	↓**	↓*	↓.	ns	ns	ns
FG	ns	↓*	↓.	↓*	ns	ns	ns	ns	ns	ns	↓*	↓.	ns	ns	↑**	↑**	↑***	↑.	↑*	ns	ns	ns	↓***	↓***	ns	ns	↑*	↑**
Season	**	*	ns	ns	*	.	**	*	***	***	.	ns	*	*	**	*	ns	.	***	*	ns	ns	ns	↓*	***	.	ns	ns
Season x Canopy	--	**	--	ns	--	ns	--	*	--	**	--	ns	--	**	--	ns	--	ns	--	.	--	ns	--	**	--	ns	--	ns
Season x Biomass	--	ns	--	ns	--	ns	--	.	--	ns	--	.	--	ns	--	ns	--	.	--	***	--	.	--	ns	--	ns	--	ns
Season x Mo	ns	ns	ns	ns	ns	ns	ns	ns	**	ns	ns	***	ns	ns	ns	ns	ns	ns	***	ns	ns	.	ns	.	ns	ns	ns	ns
Season x SR	ns	**	ns	ns	ns	ns	ns	ns	.	ns	ns	*	*	ns	ns	ns	ns	ns	ns	ns	ns	**	*	***	ns	ns	ns	***
Season x FG	**	***	ns	ns	ns	ns	ns	ns	ns	ns	.	ns	ns	*	ns	ns	.	ns	ns	ns	*	**	*	*	ns	ns	ns	*

Trifolium repens

Model	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
R ² statistics	0.72	0.96	0.62	0.99	0.69	0.86	NA	NA	0.34	0.57	0.92	0.95	NA	NA	0.77	0.85	NA	NA	0.54	0.63	0.63	0.71	0.77	0.84	0.57	0.91	0.55	0.62
Canopy	--	↓***	--	ns	--	ns	--	--	--	ns	--	↓***	--	--	--	↑***	--	--	--	ns	--	↓***	--	↓.	--	↓***	--	↑**
Biomass	--	ns	--	ns	--	ns	--	--	--	↓*	--	↓*	--	--	--	↑**	--	--	--	ns	--	↓*	--	ns	--	ns	--	↑*
Mo	↓**	↓**	ns	↓*	↓*	↓.	--	--	ns	ns	↓**	ns	--	--	↑**	ns	--	--	ns	ns	↓**	ns	↓***	↓***	↓*	ns	↑*	ns
SR	↓**	↓*	ns	↓*	↓*	↓**	--	--	ns	ns	↓.	↓***	--	--	↑*	ns	--	--	ns	ns	↓**	↓.	↓.	ns	ns	ns	↑*	ns
FG	ns	ns	ns	ns	↓*	↓**	--	--	↓.	ns	ns	↓*	--	--	ns	ns	--	--	↑.	ns	ns	↓.	ns	ns	↓*	↓*	ns	↑*
Season	**	ns	***	***	--	--	--	--	--	--	***	***	--	--	***	ns	--	--	*	ns	*	ns	ns	ns	ns	**	**	.

Season x Canopy	--	***	--	ns	--	--	--	--	--	--	ns	--	--	--	ns	--	--	--	*	--	ns	--	ns	--	***	--	ns	
Season x Biomass	--	ns	--	ns	--	--	--	--	--	--	ns	--	--	--	ns	--	--	--	ns	--	ns	--	*	--	.	--	ns	
Season x Mo	ns	ns	ns	ns	--	--	--	--	--	--	*	ns	--	--	ns	ns	--	--	ns	ns	ns	ns	ns	ns	ns	ns	ns	
Season x SR	ns	*	ns	ns	--	--	--	--	--	--	ns	ns	--	--	ns	ns	--	--	.	ns	ns	ns	ns	ns	ns	ns	ns	
Season x FG	ns	ns	ns	ns	--	--	--	--	--	--	**	.	--	--	ns	ns	--	--	*	*	ns	ns	ns	ns	.	**	ns	
<i>Vicia cracca</i>																												
Model	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
R ² statistics	0.59	0.87	0.68	0.77	NA	NA	0.79	0.84	0.69	0.74	0.44	0.80	0.44	0.60	0.72	0.74	0.76	0.79	0.47	0.85	0.69	0.79	0.49	0.65	0.47	0.86	0.70	0.76
Canopy	--	↓***	--	↑.	--	--	--	ns	--	ns	--	↓*	--	↓.	--	↑***	--	↑***	--	↑**	--	ns	--	↓*	--	↓***	--	ns
Biomass	--	ns	--	ns	--	--	--	↓*	--	↓*	--	↓.	--	↓*	--	ns	--	↑*	--	↑*	--	ns	--	↓**	--	ns	--	ns
Mo	ns	ns	↓**	↓**	--	--	↓***	↓***	↓***	↓***	↓.	ns	ns	ns	ns	↑*	ns	ns	↑.	ns	↑*	↑.	↓*	ns	↓*	↓*	↓**	↓**
SR	↓*	ns	ns	↓*	--	--	ns	ns	ns	ns	↓**	↓**	ns	ns	ns	ns	↑*	ns	↑**	↑**	↑.	↑**	↓**	↓*	ns	ns	ns	↓**
FG	↓*	ns	↓.	.	--	--	ns	ns	ns	ns	ns	ns	ns	ns	ns	↑.	ns	ns	ns	ns	↑.	ns	ns	ns	ns	ns	ns	ns
Season	**	*	***	**	--	--	*	**	ns	*	ns	*	**	**	***	*	***	*	ns	***	***	***	ns	ns	ns	***	***	*
Season x Canopy	--	*	--	*	--	--	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns	--	ns
Season x Biomass	--	ns	--	ns	--	--	--	ns	--	ns	--	**	--	ns	--	ns	--	ns	--	*	--	.	--	ns	--	***	--	ns
Season x Mo	ns	ns	ns	*	--	--	***	**	*	.	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	**	ns	*	ns	.	ns	**
Season x SR	ns	ns	.	ns	--	--	ns	ns	ns	ns	ns	*	.	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	*	ns
Season x FG	*	ns	ns	ns	--	--	ns	ns	ns	.	ns	.	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	*	ns	ns

Models were fitted by stepwise inclusion of variables. Listed are the results of likelihood ratio tests that were applied to assess model improvement and the statistical significance of the variables, where . $P \leq 0.10$, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$. R² statistics is based on likelihood ratio test statistics in comparison to the intercept-only model. The first column for each trait shows models (= model A) where only the experimental factors were fitted, the second column for each trait shows models (= model B) where canopy height and community biomass were fitted before the experimental factors. Note that the number of replicates was too low to include both covariates in models for *T. dubium*. Here, we separately tested each canopy height and community biomass and selected the model with the larger R². Arrows indicate a significant increase (↑) or decrease (↓) of trait values with increasing community diversity, biomass or canopy height. Dashes indicate absence of measurements or terms not fitted in the respective model. For abbreviations see Table 3.

Figure S1: Foliar $\delta^{15}\text{N}$ values of (a) *Lolium perenne* and (b) *Taraxacum officinale* used as non- N_2 -fixing reference species with the ^{15}N natural abundance method plotted against sown species number. All values are plot means of values measured in samples collected in June (before first mowing) and August (before second mowing) 2006. The lines are arithmetic means for values per species-richness level.

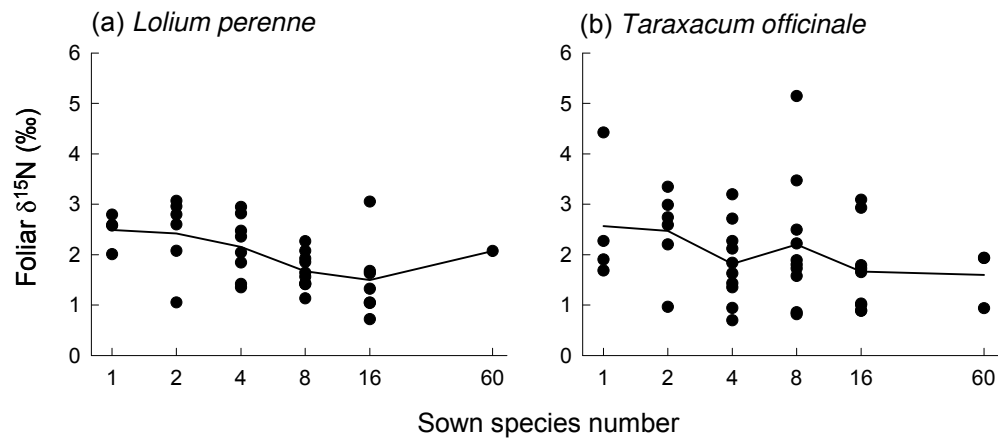


Figure S2: Trait values in mixtures (Mix) plotted against trait values in monocultures (Mono). All values are means of values measured in June (before first mowing) and August (before second mowing). Monoculture values are averaged between two replicated plots per species. Values above the diagonal line indicate cases where trait values in mixtures were larger than in monoculture. For species symbols see Fig. 3.

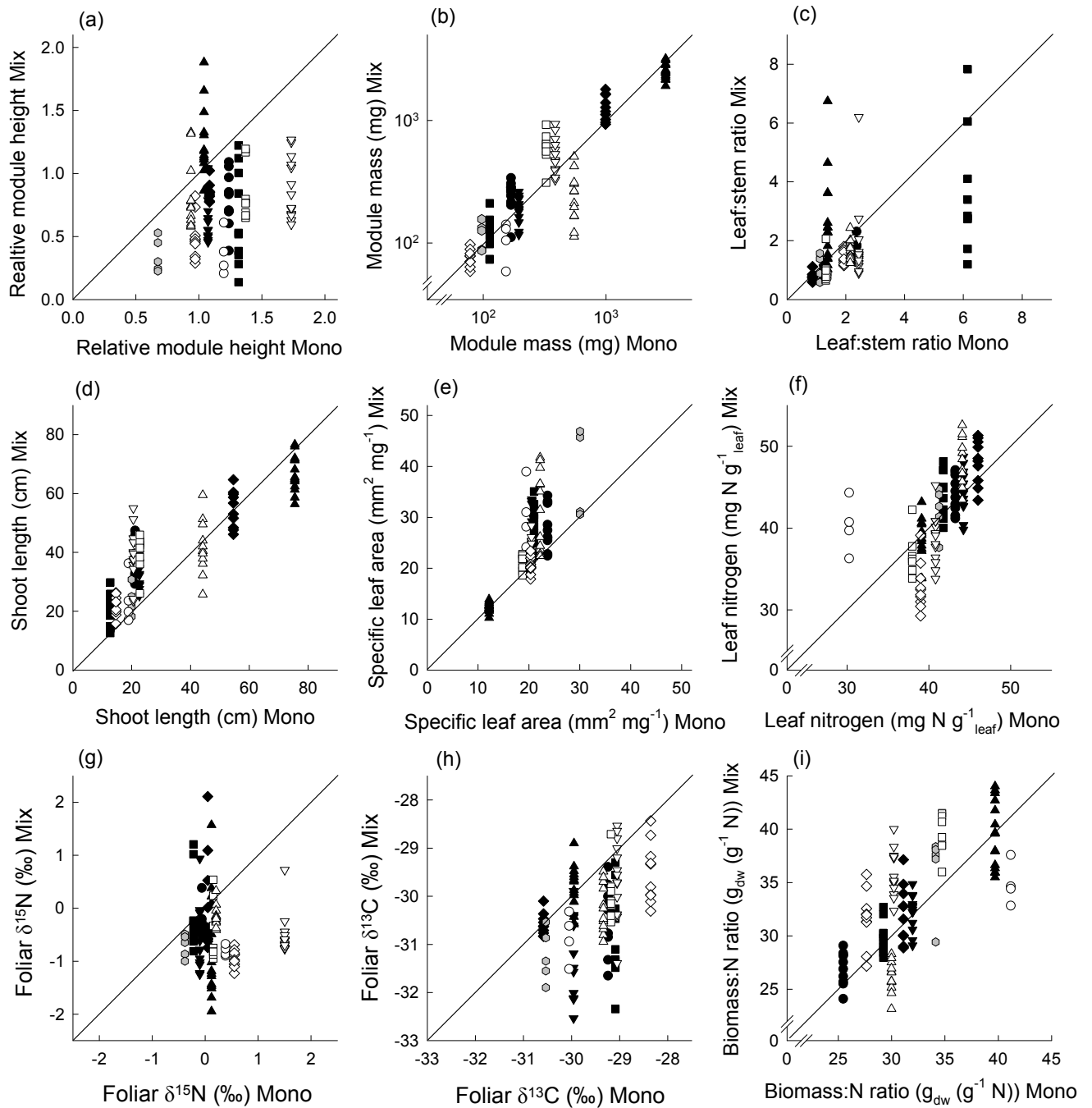


Figure S3: Trait values per species averaged across all plots (mean \pm SE) in late summer (before second mowing: Aug) plotted against trait values in early summer (before first mowing: June). For species symbols see Fig. 3.

